Floating nurseries? Scyphozoan jellyfish, their food and their rich symbiotic fauna in a tropical estuary

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Background. The anthropogenic modification of trophic pathways is seemingly prompting the increase of jellyfish populations at the expense of planktivorous fishes. However, gross generalizations are often made because the most basic aspects of trophic ecology and the diverse interactions of jellyfish with fishes remain poorly described. Here we inquire on the dynamics of food consumption of the medusoid stage of the scyphozoan jellyfish *Stomolophus meleagris* and characterize the traits and diversity of its symbiotic community.

Methods. *S. meleagris* and their associated fauna were sampled in surface waters between November 2015 and April 2017 in Málaga Bay, an estuarine system at the Colombian Pacific. Stomach contents of medusae were examined and changes in prey composition and abundance over time analysed using a multivariate approach. The associated fauna was identified and the relationship between the size of medusae and the size those organisms tested using least-square fitting procedures.

Results. The presence of *S. meleagris* medusa in surface waters was seasonal. The gut contents analysis revealed that algae, copepods and fish early life stages were the more abundant items, and PERMANOVA analysis showed that the diet differed within the seasons ($P_{(perm)}$=0.001) but not between seasons ($P_{(perm)}$=0.134). The majority of the collected medusae (50.4 %) were associated with individuals of 11 symbiotic species, 95.3% of them fishes, 3.1% crustaceans and 1.6% molluscs. Therefore, this study reports 10 previously unknown associations. The bell diameter of *S. meleagris* was positively related to the body sizes of their symbionts. However, a stronger fit was observed when the size relationship between *S. meleagris* and the fish *Hemicaranx zelotes* was modelled.

Discussion. The occurrence of S. meleagris was highly seasonal, and the observed patterns of mean body size through the seasons suggested the arrival of adult medusae to the estuary from adjacent waters. The diet of *S. meleagris* in the study area showed differences with previous reports, chiefly because of the abundance of algae that are seemingly ingested but not digested. The low number of zooplanktonic items in gut contents suggest the contribution of alternative food sources not easily identifiable. The observed changes in the composition of food in the guts probably reflect seasonal changes in the availability of prey items. The regular pattern in the distribution of symbionts among medusae (a single symbiont per host) and the positive host-symbiont size relationship reflects antagonistic intraspecific and interspecific behaviour of the symbiont. This strongly suggest that medusa represent an "economically defendable resource" that potentially increases the survival and recruitment of the symbionts to the adult population. We argue that, if this outcome of the symbiotic association can be proven, scyphozoan jellyfish can be regarded as floating nurseries.

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Abstract

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Introduction

The magnitude and frequency of population blooms of jellyfish (pelagic cnidarian and ctenophores) are seemingly increasing, along with strong impacts on marine ecosystems. The collapse of formerly rich fisheries has been linked to increasing jellyfish populations in several regions (Lynam *et al.*, 2006; Brodeur, Ruzicka & Steele 2011). However, much of the societal and

75   even scientific perception about jellyfish and their role in ecosystems is based on speculation,
76   limited evidence and flawed scientific practices (e.g. Haddock 2008; Richardson *et al.*, 2009; Sanz-
77   Martín *et al.*, 2016). Trophic interactions between jellyfish and planktivorous fishes have been
78   characterized as a combination of mutual predation and competition for planktonic food (Purcell
79   & Arai, 2001; Lynam, 2006; Brodeur *et al.*, 2008; Richardson *et al.*, 2009). Changes in the balance
80   of these trophic pathways in stressed and overfished ecosystems have been hypothesized to explain
81   massive local proliferations of jellyfish that displace planktivorous fishes and form alternate
82   jellyfish-dominated ecosystems (Richardson *et al.*, 2009). However, trophic relationships are only
83   known for a small portion of this polyphyletic assemblage spanning more than 2000 species
84   (Fleming *et al.*, 2015). As a result, trophic models assessing food web structure and energy flow
85   often ignore jellyfish or include them as a single functional group with the characteristics of an
86   'average' jellyfish whose parameterization frequently varies greatly among models (Pauly *et al.*,
87   2009). In fact, the hypotheses proposed to explain changes in jellyfish dominated ecosystems
88   remain untested, partially because there is a recognition that more basic research on feeding
89   ecology is still required (Pauly *et al.*, 2009; Richardson *et al.*, 2009; Naman *et al.*, 2016).

90   Regarding scyphozoan jellyfish, two emerging issues are challenging the predominant view of
91   competitive trophic interactions between planktivorous fishes and jellyfish. First, recent
92   methodological approaches have shown that scyphozoans use unsuspected food sources, including
93   benthic organisms (Pitt *et al.*, 2008; Ceh *et al.*, 2015), microplankton and resuspended organic
94   matter (Javidpour *et al.*, 2015). These food sources have been traditionally overlooked, because
95   most studies on feeding ecology use gut content analysis that focuses on mesozooplankton and
96   ichthyoplankton, presumably because they are more visible and retained in the gut for longer than
97   other type of food (Pitt, Connoly & Meziane, 2009). Thus, the widely held view that fishes and
98   scyphozoan jellyfish compete for the same food source seems a gross generalization. Second,
99   mounting evidence suggests that mutual predation (i.e, medusae predating on fish egg or larvae
100   and fishes predating on medusae early life stages) is only one side of the story. Scyphozoans
101   usually display "symbiotic associations", defined as any living arrangement, including positive
102   and negative associations, between members of two different species (see Martin and Schwab
103   2013). Symbionts are diverse, ranging from fish to invertebrates, in a variety of relationships
104   including parasitism, mutualism and commensalism (Riascos, 2013; Ohtsuka *et al.*, 2009; Ingram,
105   Pitt & Barnes 2017). However, trophic modelling efforts traditionally focus on predation and
106   competition, despite mounting evidence showing that alternative trophic pathways and
107   relationships may positively affect fish populations (e.g. Lynam & Brierley, 2007; Riascos *et al.*,
108   2012; Greer *et al.*, 2017).

109   Much of the prevalent view about fish-jellyfish trophic dynamics is derived from scyphozoans of
110   subtropical and temperate areas that support large pelagic fisheries. In estuarine systems, the scarce
111   evidence suggests a low trophic overlap between fish and jellyfish (Nagata *et al.*, 2015; Naman *et*
112   *al.*, 2016) and a high occurrence of symbiotic associations with juveniles of fish and invertebrates
113   (e.g., Rountree 1983; Costa, Albieri & Araújo, 2005; Martinelli *et al.*, 2008), perhaps reflecting
114   the abundance of early stages of coastal fauna in nursery areas. Hence there is a need to study the
115   trophic ecology of scyphozoan jellyfish and their multiple biological interactions to truly
116   understand population dynamics, their position in food webs and their functional role in estuarine
117   ecosystems.

118   Here we studied the canonball jellyfish *Stomolophus meleagris* (Agassiz, 1862), in the estuarine
119   ecosystem of Malaga Bay, an area of high biodiversity in the Colombian pacific coast. This species

120 is widely distributed in the western Atlantic (United States to Brazil) and the Pacific oceans
121 (southern California to Ecuador; Sea of Japan to South China Sea) (Calder, 1982; Griffin &
122 Murphy, 2011) and has been described as a specialized predator of fish eggs, copepods and mollusc
123 larvae, with the capacity to regulate local populations of its prey (Larson, 1991). Therefore, the
124 aims of this study were (i) to assess changes in the structure of the diet in the study area and (ii)
125 analyse the traits, diversity and significance of the symbiotic associations in the estuarine
126 ecosystem.

127

Materials & Methods

128

129 Sampling

130 The study was performed in Málaga Bay, a south-facing bay located in the central region of the
131 Colombian Pacific coast (4°05′ N and 77°16′ W, Fig. 1). The bay is located within the Chocó-
132 Darien region, an area with one of the highest levels of precipitation in the western hemisphere
133 (7,000–11,000 mm; Poveda, Jaramillo & Vallejo, 2014), which has two wet seasons during the
134 year: April-June and September-November. The water depth in this bay averages 13 m but reaches
135 a maximum of 40 m. Tides are semi-diurnal, with a mean tidal range of 4.1 m. Sea surface
136 temperature varies between 25 and 30 °C and salinity between 19 and 28 in the mouth of the bay
137 and 1.3 and 10 close to small rivers (Lazarus and Cantera 2007). Sampling of *S. meleagris* was
138 conducted around La Plata Archipielago, at the innermost part of Málaga Bay. Samplings were
139 allowed by the Autoridad Nacional de Licencias Ambientales (ANLA; permit number 1070_28-
140 08-2015). The medusoid phase showed a seasonal occurrence in surface waters: December 2015
141 to May 2016 (hereafter season 1) and December 2016 to April 2017 (hereafter season 2). Sampling
142 effort was relatively constant throughout the seasons: when medusae were detected, three or four
143 3-hour sighting trips were performed per month. Medusae were sampled from a small boat using
144 dip nets, and the relative abundance was estimated as the number of caught medusae per hour. As
145 medusas where generally associated to juvenile fish or invertebrates the sampling was limited to
146 15 to 20 medusae per month, to avoid disturbing populations of fish potentially under conservation.
147 Upon collection, medusae discharged a sticky mucus that rapidly killed fish or associated
148 invertebrates as reported by Shanks & Graham (1988). Thereafter, medusae and their associated
149 fauna were tagged and stored in individual jars with 5% borate buffered formaldehyde solution in
150 seawater.

151 In the laboratory, the bell diameter of each medusa and the standard length of associated fish and
152 invertebrates (crustaceans and molluscs) were measured using callipers. The medusa′s fused oral
153 arms and the mouth folds were excised and rinsed through a 100-μm mesh sieve to concentrate
154 food particles. The resulting material was transferred to ethanol and sorted for the presence of prey
155 items using a dissecting microscope. Prey items were determined to a taxonomic level suitable for
156 making meaningful comparisons with similar studies (Larson 1991; Padilla-Serrato *et al.*, 2013;
157 Álvarez-Tello, López-Martínez, & Lluch-Cota, 2016).

158 Associated fish were identified to species according to current keys and by comparison of their
159 morphological features against available descriptions (Jordan & Evermann 1898; Allen &
160 Robertson 1994; Fischer *et al.*, 1995, Chirichigno & Cornejo, 2001, Robertson & Allen, 2005).
161 Molluscs and crustaceans were identified by Cantera JR and JF Lazarus, respectively. Finally, all

162 the associated fauna was stored as reference material in the scientific collection at the Marine
163 Biology section at Universidad del Valle.

164 Data analyses

165 A multivariate approach was used to test changes in the structure (composition and abundance) of
166 the diet over time. For this, data were arranged in a matrix of abundance of each taxon (rows) eaten
167 by individual medusae in each month (columns). Prey taxa with few occurrences (< 0.1% of total
168 abundance; Table 1), were excluded from further analyses. Prior to the analyses data were
169 standardized to account for the difference in food quantity associated to distinct medusae body
170 sizes, by dividing the abundance of each prey item by the total abundance of prey for each medusa.
171 Moreover, data were square root transformed to slightly downweigh the contribution of abundant
172 food items.

173 Non-metric multidimensional scaling (nMDS; Clarke & Gorley 2006) was used to build an
174 ordination plot of medusae per month and season calculated from a Bray–Curtis matrix of
175 similarity in diet composition. The distance-based permutational multivariate analysis of variance
176 (PERMANOVA, Anderson 2001) was used to test for temporal differences in the structure of diet
177 between months and seasons. The model used "month" as a random factor nested within the fixed
178 factor "season". As the PERMANOVA approach is sensitive to differences in multivariate
179 dispersion within groups, the PERMDISP routine was used to test for homogeneity of dispersions.
180 Thereby, a preliminary analysis showed that multivariate dispersion was strongly dependent of
181 sample size, with less dispersion observed at the beginning of the season, when medusae were
182 scarce in the field and thus sample size was smaller. Therefore, samples from December 2015
183 (N=2) January 2015 (N=2) and January 2016 (N=5) were excluded from the analysis. Finally,
184 when temporal differences were confirmed by the PERMANOVA, a Canonical Ordination of
185 Principal Coordinates (CAP, Anderson & Wills 2003) was used as a constrained ordination that
186 best defines groups (months) according to the diet structure.

187 To assess if the body sizes of medusae and their symbionts are related, length data were fitted to
188 linear, polynomial, logarithmic, exponential and power models. The best fit was chosen according
189 to the proportion of variance explained. Models were fitted by least squares procedures using the
190 algorithm Levenberg-Marquardt to estimate standard errors (SE) of the parameters. Finally, we
191 performed a literature review of the reported symbiotic fauna for *S. meleagris* to compare the
192 diversity of associations found in the study area. The terms "*Stomolophus*" and "*Stomolophus*
193 *meleagris*", excluding the terms "venom", "protein" and proteomics" from the title or in
194 combination with "association", "symbiosis" or "relationship", were used to search the ISI Web
195 of Science database and Google Scholar. The resulting literature was then manually scanned for
196 descriptions of symbiotic relationships

197

198 **Results**

199 1. Jellyfish seasonality

200 Two species of scyphozoan jellyfish were found during this study: *S. meleagris* and *Pelagia*
201 *noctiluca*. The latter was found only occasionally; one individual during season 1 and six during
202 the season 2. Such a small sample size circumvents any quantitative analysis and therefore only
203 descriptive details will be given. The relative abundance of *S. meleagris* consistently showed a

204   unimodal pattern with peaks during March or April (Fig. 2). Moreover the bell diameter did not
205   show a consistent pattern of growing or decreasing size over time.

206   2. The dynamics of food consumption by *S. meleagris*

207   The composition and abundance of food items consumed by *S. meleagris* is shown in Table 1. The
208   diet was prevalently comprised of bacillariophyte algae, copepods and fish early stages. Small
209   amounts of benthic items (e.g., juvenile polychaetes, amphipods and adult *Emerita* sp) were found
210   frequently and suggest that *S. meleagris* feeds near the bottom. A few nematods, typically jellyfish
211   parasites, were also found but included as food items because they were not buried in the host's
212   tissue, as observed by Phillips & Levin (1973), and showed obvious signs of digestion. Arguable

213   Between-month differences in diet composition were apparent form the nMDS ordination (Fig. 3),
214   particularly when the same month from different seasons were compared (e.g. March in each
215   season). However, as the PERMDISP test was significant for the factor "month" ($F_{9,111}$ = 4.242;
216    $P_{(perm)}$ = 0.006), a PERMANOVA might yield misleading results. To circumvent this problem,
217   months with small sample sizes (N≤ 5) were excluded (PERMDISP test not significant: month:
218    $F_{6,105}$ = 2.183; $P_{(perm)}$ = 0.066; season: $F_{1,110}$ = 1-734; $P_{(perm)}$ = 0.211).

219   The PERMANOVA analysis (Table 2A) showed significant differences in the structure of the diet
220   of *S. meleagris* among months ($P_{(perm)}$=0.001) but not between seasons ($P_{(perm)}$=0.134). Pair-wise
221   comparisons (Table 2B) revealed between-month differences, which were best illustrated by the
222   CAP constrained ordination (Fig. 4). Scyphozoan jellyfish are widely considered carnivore
223   predators and, as such, the inclusion of phytoplankton items in the analysis of diet composition
224   seems unwarranted and the described dynamics of food consumption questionable. Therefore, the
225   PERMANOVA analysis was re-run with exclusion of the Coscinodiscophyceae and
226   Bacillariophyceae. This analysis rendered remarkably similar results: significant differences in the
227   structure of the diet among months ($P_{(perm)}$=0.002) but not between seasons ($P_{(perm)}$=0.128)
228   (Supplemental Table S1).

229   3. Traits and diversity of the biological associations

230   The body size of the 121 collected *S. meleagris* ranged between 12.1 and 109.2 mm in bell
231   diameter. The prevalence of symbiotic associations (i.e., the percentage of medusa harbouring
232   symbionts) was high, with 50.4% of the collected specimens. With only three exceptions, a single
233   symbiont per medusa was found, clearly indicating that the distribution of symbionts among host
234   was not random but uniform. The symbiotic community of *S. meleagris* was composed of fishes
235   (95.3%), crustaceans (3.1%) and molluscs (1.6%) (Figure 5). Generally, associated fish reacted to
236   disturbance by hiding within oral arms or below the host´s bell; it could be said that fish "resist
237   efforts to separate them", as stated by Hargit (1905). However, the prevalence of symbiotic
238   association might have been underestimated, because some may have escaped during the sampling.
239   Regularly only one symbiont per host was found, with only three exceptions, where two fish per
240   medusa where observed. *P. noctiluca* also had symbiotic associations: two out of six medusae
241   harboured individual fish (*Hemicaranx zelotes*).

242   The body size of the scyphozoan *S. meleagris* showed a significant positive correlation with the
243   body size of its symbiotic community as a whole, the fish assemblage and *H. zelotes* in particular
244   (Fig. 5; Table 3). Power models best fitted the positive body size relationships, and the model
245   including only *H. zelotes* had the highest proportion of variability explained (0.634). This partially

246   reflects the fact that *H. zelotes* was the most common symbiont of *S. meleagris*. Figure 5 shows
247   that the symbionts were generally smaller than the host. However, less frequent symbionts did not
248   follow that pattern; for instance, *Centropomus medius*, *Lutjanus guttatus*, *Oligoplites altus*, *Selene*
249   *brevoortii* and *Gerres similimus* were larger, and *Hyporhamphus snyderi* almost twice as large as
250   its host.

251   The richness of the symbiotic fauna reported for *S. meleagris* in the study area was unexpectedly
252   high: 11 species, 10 of them being new reports of symbionts for this species. This richness
253   represents 39.2 % of the total diversity of associations found so far (28 symbiotic species reported;
254   Table 4) for this widely-distributed scyphozoan jellyfish.

Discussion

256   The occurrence of *S. meleagris* in the study area showed a consistent seasonal pattern that
257   coincides with the seasonal increase in the sea surface temperature from January to May in the
258   study area (IDEAM, 2004). The body size did not show an increasing trend through the seasons.
259   This suggest that the observed medusae did not recruit from local benthic polyps, but arrive to the
260   estuarine system as adults from adjacent areas, as discussed by Kraeuter & Seltzer (1975) for S.
261   meleagris in Georgian and North Carolina waters.

262   There are only three published studies on feeding ecology of *S. meleagris*. Taken together, these
263   studies highlight that a few taxa form a high percentage of the total gut content. Larson (1991)
264   found that in the north-eastern Gulf of Mexico 98% of *S. meleagris* diet was composed of bivalve
265   veligers, tintinnids, copepods, gastropod veligers and Oikopleura (Appendicularia). In the Gulf of
266   California, off the coast of Sonora, gut contents were dominated by fish eggs (ca. 83% in a study
267   by Padilla-Serrato *et al.*, 2013; and ca. 59% in a study by Álvarez-Tello, López-Martínez, & Lluch-
268   Cota, 2016), followed by mollusc larvae (~26%) and copepods (~11%) (Álvarez-Tello, López-
269   Martínez, & Lluch-Cota, 2016). Although our results (Table 1) also show that a few items comprise
270   high percentages of the diet, the composition and relative importance of those items varied strongly
271   among studies, suggesting strong spatial-temporal differences in food composition. The main
272   difference with previous studies is the consistency of Bacillariophyta among ingested items,
273   surprising for a scyphozoan considered carnivore. However, the fact that phytoplankton items did
274   not influence the temporal patterns in the structure of gut contents suggest a level of structural
275   redundancy (i.e., many items are interchangeable in the way they define changes in composition
276   through time, sensu Clarke & Warwick, 1998) However, finding an ingested item does not mean
277   that it is digested, which is one general limitation of studying feeding patterns of jellyfish by gut
278   contents (Pitt, Connolly & Meziane, 2009). As Bacillariophyceae (*Nitzschia*) and
279   Coscinodiscophyceae (*Coscinodiscus, Rhizosolenia*) are among the most abundant phytoplankton
280   components in Málaga Bay (Prahl, Cantera & Contreras, 1990), it seems reasonable to apply
281   Ockham´s principle and assume that the presence of algae in gut contents only reflect their
282   abundance in the water column. Interestingly, Larson (1991) also states that "*Coscinodiscus* sp.
283   was abundant in gut contents" but it was not listed as prey taxa. It is worth noting that the
284   assumption that jellyfish feed on mesozooplankton and ichthyoplankton is probably related with
285   the essentially arbitrary use of 60-100 µm sieves to concentrate the samples for gut content
286   analysis. In fact, when alternative methods like grazing experiments, microvideographic
287   techniques, stable isotopes and fatty acid tracers are used it becomes apparent that jellyfish can
288   also feed on microzooplankton (Sullivan & Gifford, 2004; Colin *et al.*, 2005), demersal

289 zooplankton (Pitt *et al.*, 2008) and resuspended organic matter (Javidpour *et al.*, 2015). Therefore,
290 our results should be regarded as a partial depiction of the diet composition of *S. meleagris*.

291 As body size of *S. meleagris* did not show a consistent pattern of growth over time (Figure 2), the
292 intra-season variability observed in the structure of the diet could not be attributed to ontogenetic
293 changes in food habits. In fact, the diet composition of the smaller and larger medusae observed
294 in December 2015 and January 2016, respectively, (Fig. 2), was very similar (Fig. 3). Therefore,
295 the observed intra-season variability might be related with changes in the availability of prey in
296 the water column, but information to evaluate this hypothesis is lacking.

297 The lack of significant differences in the diet structure of *S. meleagris* between seasons was
298 surprising because the first medusoid season coincided with the major El Niño-La Niña cycle
299 2015-2016, which heavily modified temperature and rainfall patterns in the study area (Riascos,
300 Cantera & Blanco-Libreros, 2018). For example, it is known that the strong modification of
301 freshwater nutrient subsidies through precipitation in Málaga Bay drives changes in the population
302 dynamics and reproductive cycle of benthic estuarine bivalves (Riascos 2006; Riascos, Heilmayer
303 & Laudien, 2008). Hence, it would be reasonable to expect shifts in the abundance and composition
304 of the zooplankton community associated to El Niño-La Niña 2015-2016 during the first season,
305 which would be then reflected in significant changes in the diet structure of *S. meleagris* between
306 seasons. It is difficult to speculate on reasons for this result, but perhaps El Niño-La Niña modified
307 the composition of the zooplankton community at lower taxonomic levels (e.g., species, families),
308 which we were not able to detect owed to our categorization of prey items at higher taxonomic
309 levels (Table 1).

310 Marshes, mangrove forests and seagrass meadows have long been recognized as nursery grounds,
311 mainly because they have extremely high primary and secondary productivity and support a great
312 abundance and diversity of early life stages of fish and invertebrates (Beck *et al.*, 2001). Recently,
313 Doyle *et al.*, (2014) analysed the role of jellyfish as "service providers" in pelagic habitats and
314 described jellyfish as habitat and nurseries, because they are: (i) larger than most planktonic
315 organisms, (ii) slower swimmers than most nektonic animals and (iii) their diverse morphology
316 provide three-dimensional space for refuge or shelter. Clearly those facts alone do not meet the
317 premise that "a habitat is a nursery for juveniles of a particular species if its contribution per unit
318 area to the production of individuals that recruit to adult populations is greater, on average, than
319 production from other habitats in which juveniles occur" (Beck *et al.*, 2001). Strictly speaking,
320 this is a hypothesis remaining to be tested, though some of our results suggest that *S. meleagris*
321 occurring in estuarine systems provide a valuable resource that may significantly increase the
322 survivorship and recruitment of juvenile fishes or invertebrates. First, the great dominance of *H.*
323 *zelotes* among a diversity of other symbionts suggest a higher suitability to its host. This is in line
324 with the fact that fish of the family Carangidae are the most commonly reported symbiont of *S.*
325 *meleagris* (Table 4). Secondly, the high prevalence of an association and a uniform distribution of
326 the symbiont within the host population as those observed for *H. zelotes* and *S. meleagris* strongly
327 suggest intraspecific and interspecific interactions and territorial behaviour (Conell, 1963;
328 Britayev *et al.*, 2007; Riascos *et al.*, 2011). And thirdly, positive symbiont-host size relationships,
329 as those observed when *H. zelotes*, the fish assemblage and the whole symbiotic assemblage are
330 analysed, suggest either parallel growth of the host and the symbiont (Britayev & Fahrutdinov,
331 1994) or size-segregation behaviour by the symbiont (Adams, Edwards & Emberton, 1985; Hobbs
332 & Munday 2004).

333 Ecological theory predicts that competition and the "economic defendability" of a resource (*sensu*
334 Brown, 1964) facilitate or hinder the evolution of territoriality; resources are monopolized
335 whenever the benefits exceed the costs of defence. Individuals of a territorial species that fail to
336 obtain a limited resource often make no contribution to future generations (Begon, Harper &
337 Townsend, 2006). For jellyfish-fish associations, there is correlational data suggesting that the
338 shelter and/or food provided by jellyfish increase the survival of juvenile fish to adulthood (Lynam
339 & Brierley, 2007). In this context, if the seasonal occurrence of *S. meleagris* does represent a
340 defendable resource, and the influence on the survival of its symbiotic fauna could be
341 experimentally demonstrated, this species may be considered a floating nursery.

342 According to Castro, Santiago & Santana-Ortega (2001) 333 species of fish belonging to 96
343 families show aggregative or associative behaviour with floating algae, gelatinous zooplankton,
344 whales, flotsam or man-made fish aggregating devices and 14 of these families associate with
345 jellyfish. Therefore, one may reasonably argue that if the jellyfish-fish association have a
346 measurable effect on fish populations, it can be considered marginal. But, how complete is our
347 knowledge of these associations? Regarding *S. meleagris*, Table 4 hints on this question. First of
348 all, it shows that only a few areas of the species distribution range have been studied, particularly
349 the western coast of United States and the Gulf of Mexico. Second, and more importantly, the fact
350 that the findings of our short-term study performed in a small tropical estuarine system represent
351 ca. 40% of the known diversity of the symbiotic fauna of *S. meleagris* strongly suggest that
352 diversity of symbionts increase toward tropical areas and that it is heavily underestimated. Indeed,
353 the seven-year monitory of the bycatch in the trawl fishery of *S. meleagris* off Georgia by Page
354 (2015), rendered 38 species of finfish and 3 species of invertebrates. Of course, these cannot per
355 se be assumed to be symbionts of *S. meleagris*. But the fact that three species known to be common
356 associates (*Peprilus paru*, *P. triacanthus* and *Chloroscombrus chrysurus*; Phillips, Burke &
357 Keener, 1969; Rountree, 1983) comprised 63% of the bycatch strongly suggest that some of the
358 other species may actually be unrecognised symbionts. To conclude, a more precise account of the
359 diversity of symbiotic fish-jellyfish associations and an evaluation of their ecological significance
360 may provide a more balanced view of the relationship between fish and jellyfish in marine
361 ecosystems.

362 **Acknowledgments**

367

368

369 **Figures**

370 Figure 1. Map of the study area in La Plata Archipelago (Málaga Bay, Colombian Pacific coast)

371 Figure 2. Monthly variability of bell diameter (grey bars) and relative abundance (black lines) of
372 *Stomolophus meleagris* in La Plata Archipelago (Málaga Bay, Colombia) during two medusoid
373 seasons A) December 2015-May 2016; B) December 2016-May 2017

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Figure 3. nMDS ordination plot on the diet composition of *Stomolophus meleagris* calculated from Bray-Curtis dissimilarity measures with square-root transformed data of abundance per food item during two medusoid seasons (December 2015-May 2016 and Jan 2017-Apr 2017)

Figure 4. Constrained Canonical Analysis of Principal Coordinates of the diet composition of *Stomolophus meleagris* calculated from Bray-Curtis dissimilarity measures with square-root transformed data of abundance per food item during two medusoid seasons (December 2015-May 2016 and Jan 2017-Apr 2017)

382

Figure 5. Body size relationships between *Stomolophus meleagris* and its symbiotic fauna. Lines represent the model fits for *Hemicaranx zelotes*, fishes and the whole symbiotic community. Parameter estimations and associated statistics for each model are given in Table 3. The dotted lined circle represents a *H. zelotes,* excluded from the analysis, as its association to the respective medusa could not be confirmed with certainty.

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Figure 1

Map of the study area in La Plata Archipelago (Málaga Bay, Colombian Pacific coast)
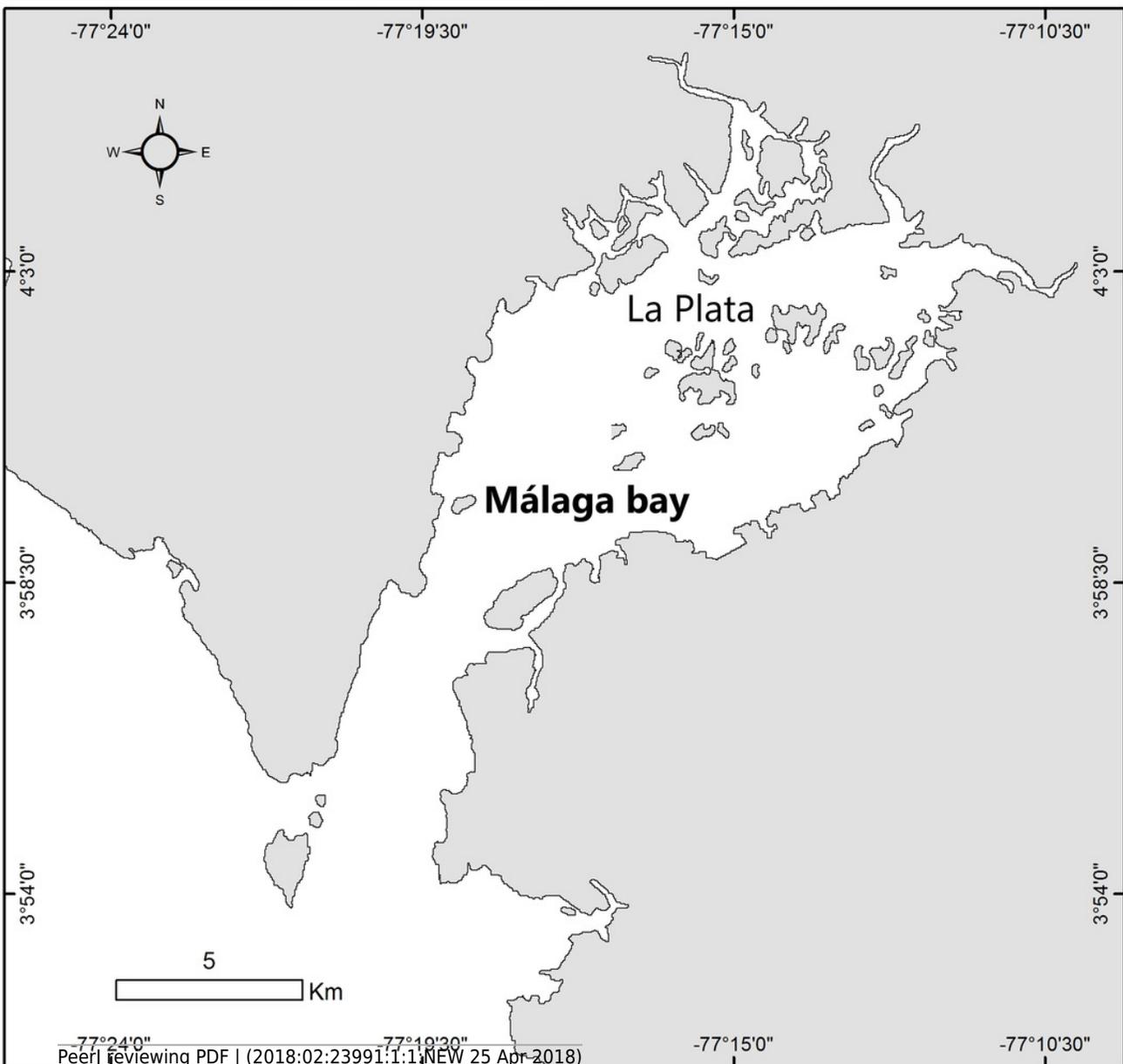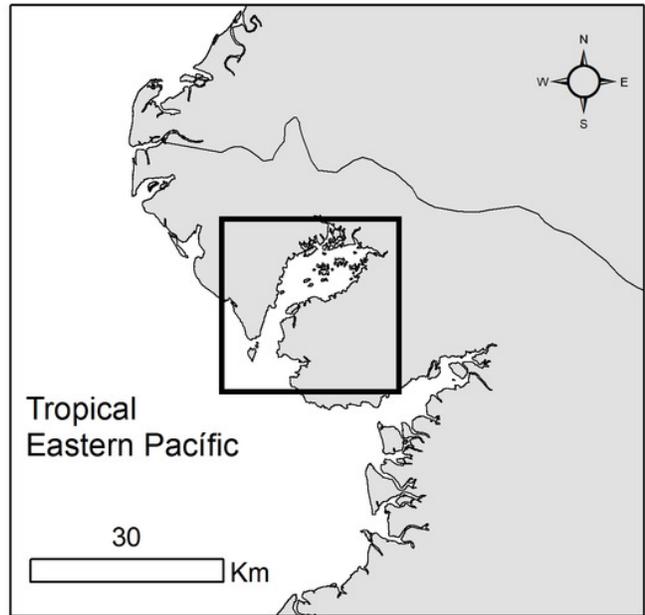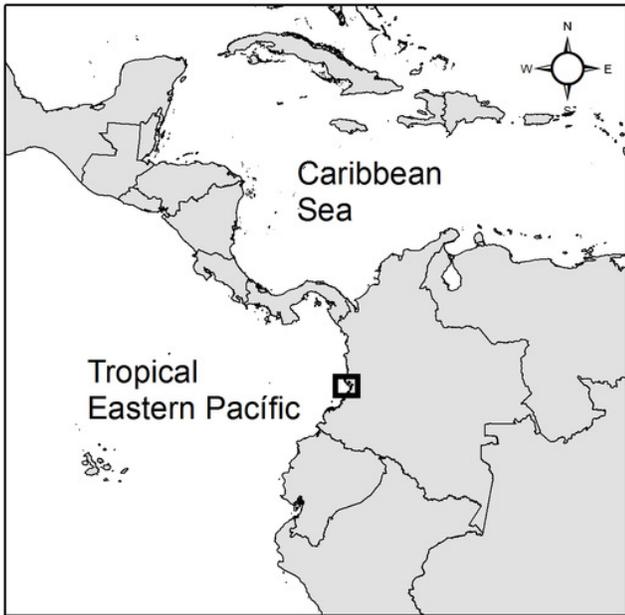
Figure 2(on next page)

Monthly variability of bell diameter and relative abundance of *Stomolophus meleagris* in La Plata Archipelago (Málaga Bay, Colombia) during two medusoid seasons

Grey bars represent bell diameter and black lines the relative abundance of Stomolophus meleagris. Seasons are: December 2015-May 2016 (A); December 2016-May 2017 (B)
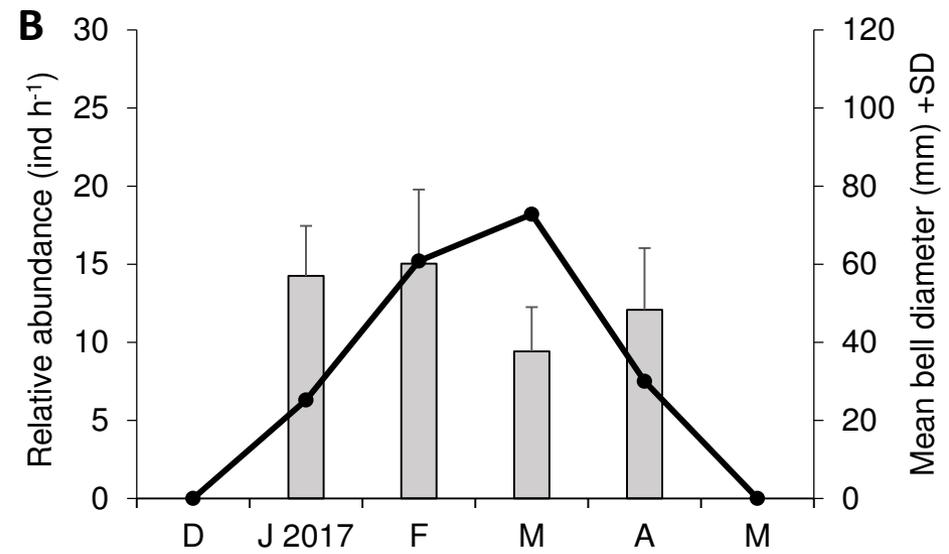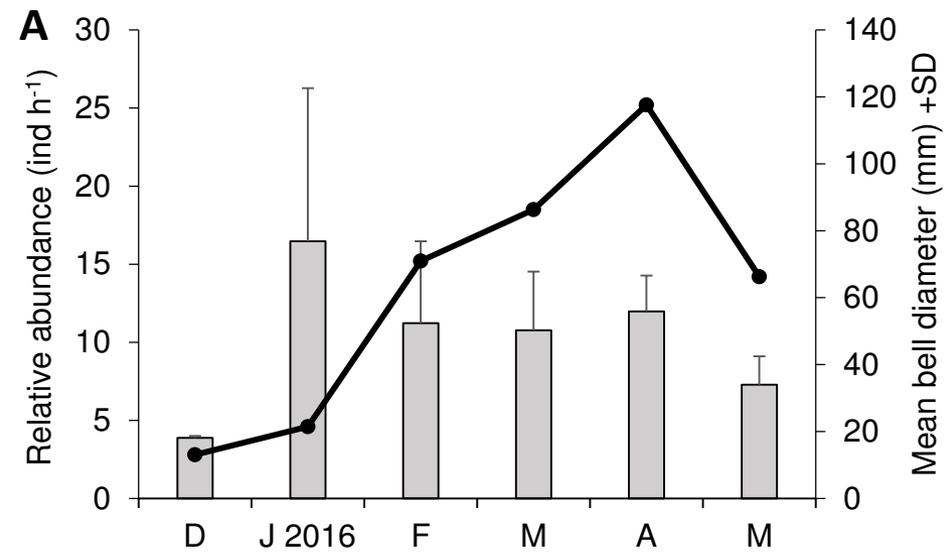
Figure 3(on next page)

nMDS ordination plot on the diet composition of *Stomolophus meleagris*

nMDS calculated from Bray-Curtis dissimilarity measures with square-root transformed data of abundance per food item during two medusoid seasons (December 2015-May 2016 and Jan 2017-Apr 2017)

2D Stress: 0.26

Season 1
▲ Dec
▼ Jan
■ Feb
◆ Mar
● Apr
✳ May

Season 2
▼ Jan
■ Feb
◆ Mar
● Apr
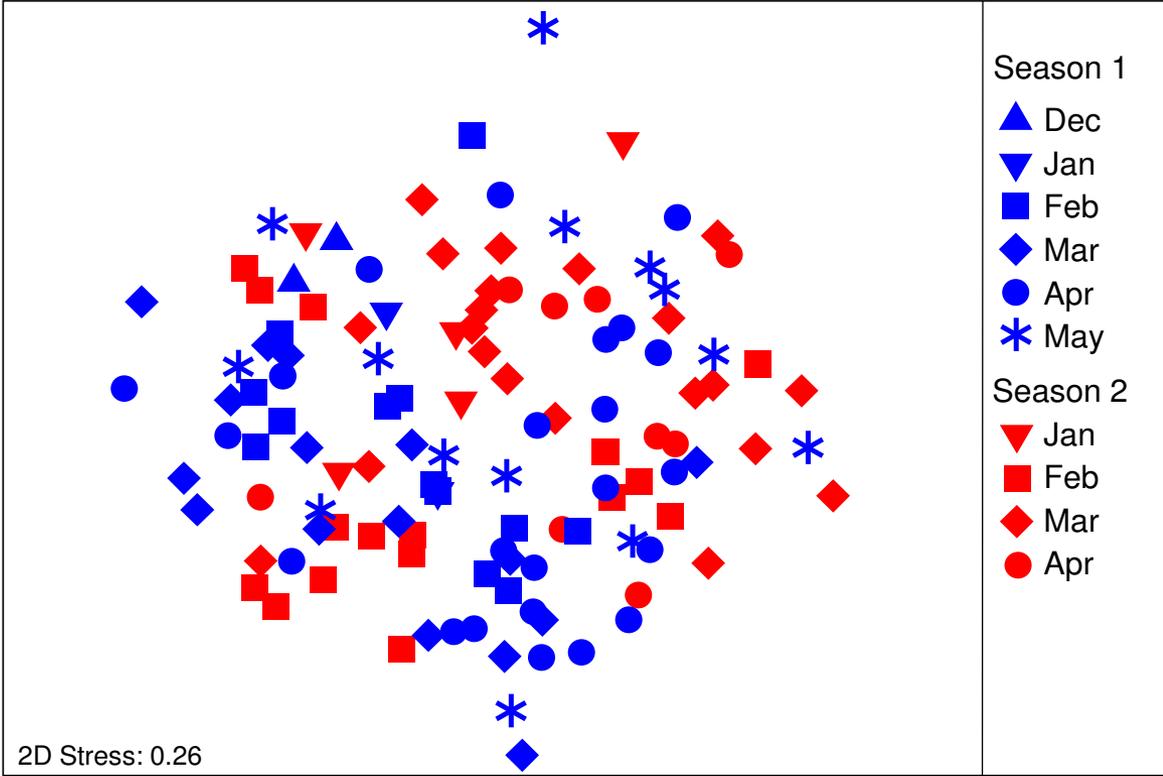
Figure 4(on next page)

Constrained Canonical Analysis of Principal Coordinates of the diet composition of *Stomolophus meleagris*

CAP analysis based in Bray-Curtis dissimilarity measures with square-root transformed data of abundance per food item during two medusoid seasons (December 2015-May 2016 and Jan 2017-Apr 2017)
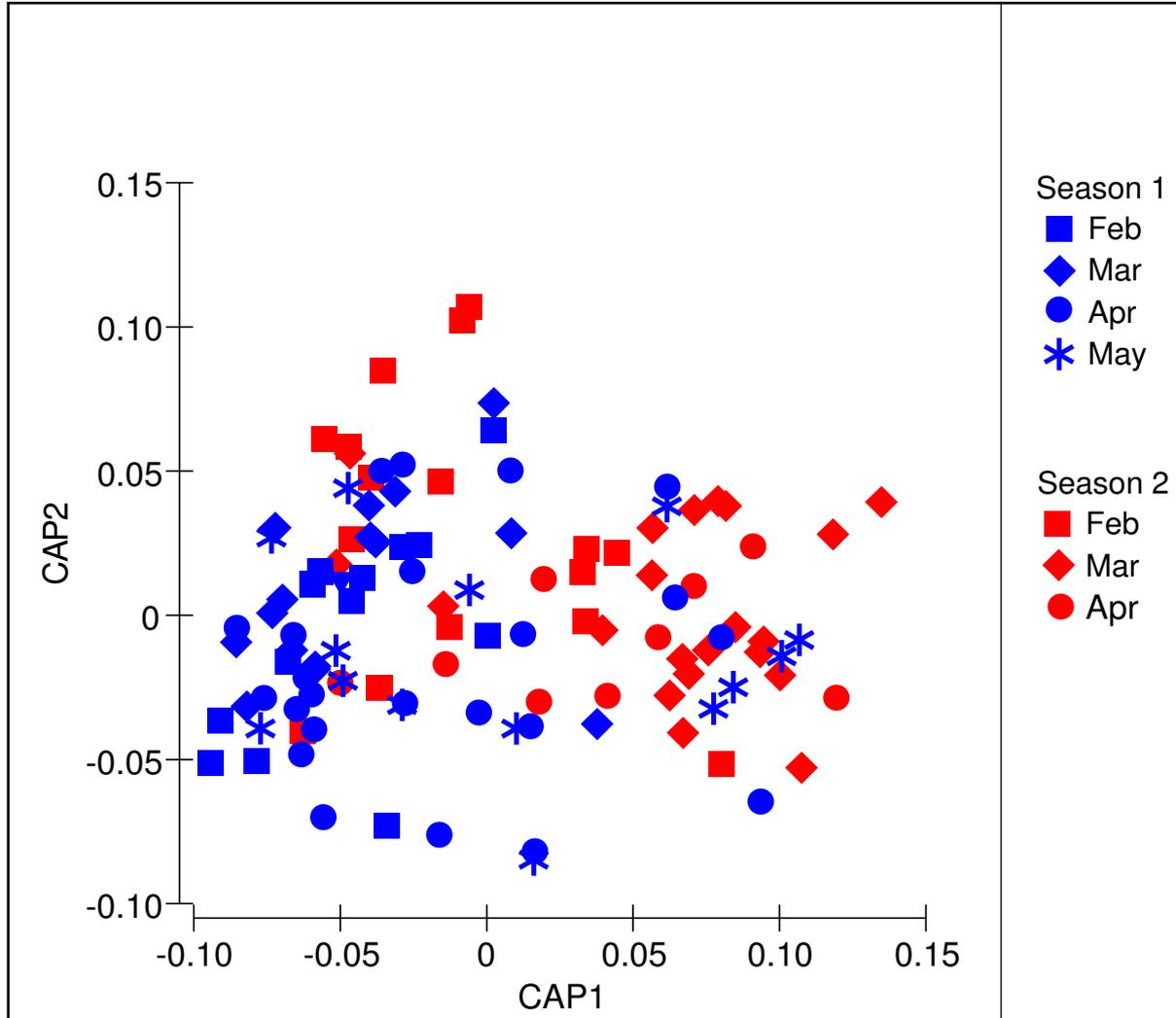
Figure 5(on next page)

Body size relationships between *Stomolophus meleagris* and its symbiotic fauna.

Lines represent the model fits for *Hemicaranx zelotes*, fishes and the whole symbiotic community. Parameter estimations and associated statistics for each model are given in Table 3. The dotted lined circle represents a *H. zelotes,* excluded from the analysis, as its association to the respective medusa could not be confirmed with certainty.
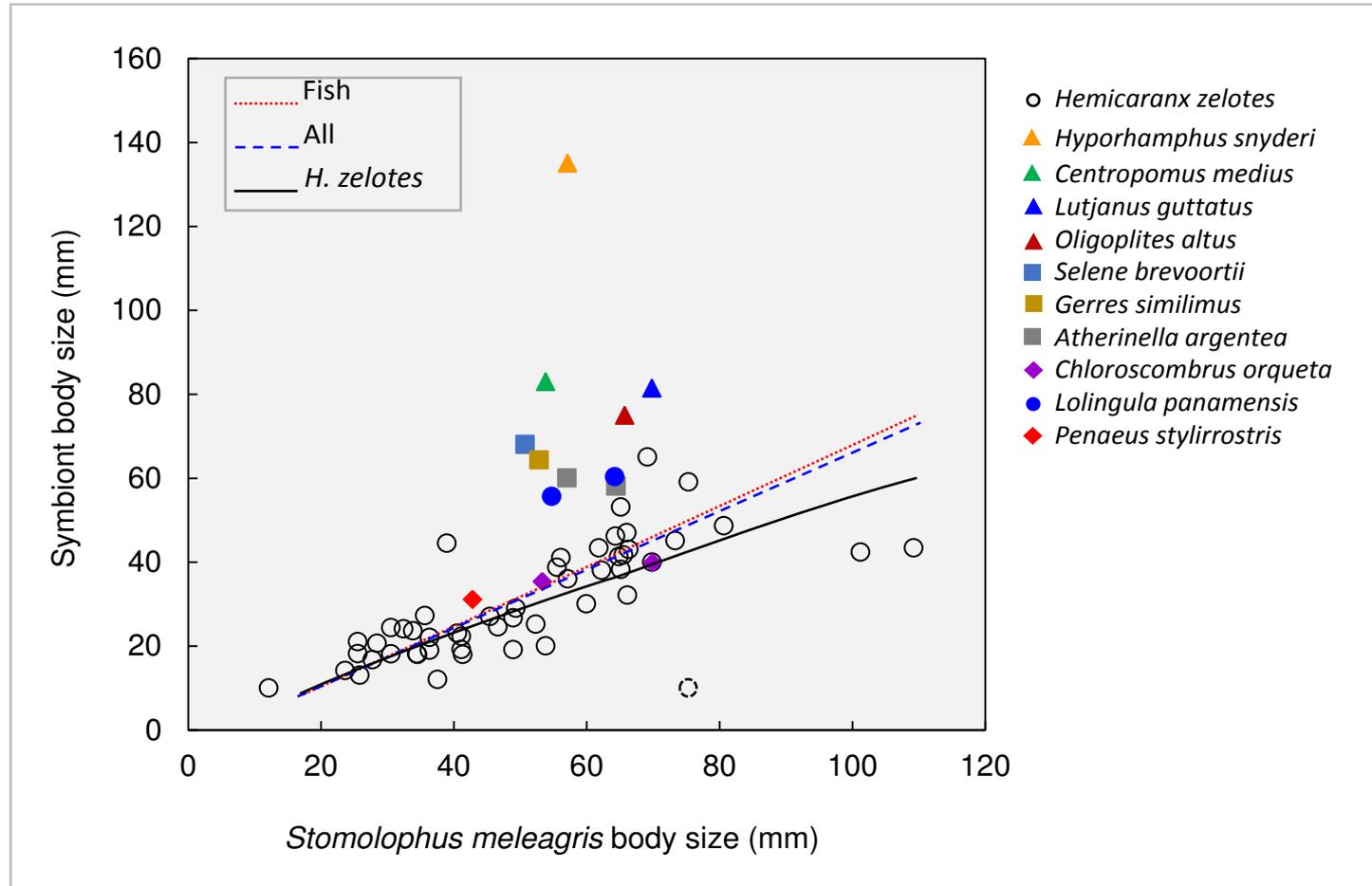
Table 1(on next page)

Composition and mean abundance (number of food item per medusa and standard error in brackets) of food items in gut contents of *Stomolophus meleagris* during two seasons in Bahía Málaga, Pacific coast of Colombia.

1 Table 1. Composition and mean abundance (number of food item per medusa and standard error in brackets) of food items in gut contents
2 of *Stomolophus meleagris* during two seasons in Bahía Málaga, Pacific coast of Colombia.

Food ítem	Season 1 (2015-2016)						Season 2 (2017)				Tot.	Rel. Ab (%)
	Dec	Jan	Feb	Mar	Apr	May	Jan	Feb	Mar	Apr		
Bacillariophyta: Coscinodiscophyceae	0 (0)	1.5 (2.1)	6.2 (9.4)	12.1 (30)	9.6 (13.2)	1.9 (4.9)	1.6 (1.9)	0.6 (0.7)	0.2 (0.5)	1.7 (3.9)	561	18.
Arthropoda: Copepoda	37.5 (14.8)	4 (5.7)	5.5 (4.8)	3.2 (3.1)	6.1 (13.8)	1.8 (1.9)	2.4 (3.8)	0.9 (1.5)	0.7 (1)	3.4 (5.2)	444	14.
Bacillariophyta: Bacillariophyceae	0.5 (0.7)	14.5 (7.8)	7.8 (15.6)	1.7 (5.2)	3.7 (6)	2.9 (5.9)	1.6 (1.7)	1.6 (2.5)	1.3 (2)	5.4 (8.1)	395	12.
Chordata: Fish (eggs & larvae)	1 (0)	6 (1.4)	3.1 (3.8)	3.6 (4.1)	3.2 (6.2)	3.9 (10.6)	0.6 (1.3)	1.9 (2.5)	0.7 (1.3)	2.1 (2.7)	308	9.
Arthropoda: Crustacea	0 (0)	0 (0)	0.9 (3.3)	0.7 (2.3)	2.7 (4.1)	1.8 (2.2)	1.6 (1.5)	1.8 (3.2)	4.3 (3.2)	5.4 (3.7)	286	9.
Mollusca: Bivalve larvae	0 (0)	2 (2.8)	2.2 (2.8)	3.7 (5)	1.9 (4.3)	0.8 (1.4)	1 (1)	2.5 (2.5)	0.6 (0.8)	2.8 (3.3)	229	7.
Mollusca: Gastropod larvae	0 (0)	6.5 (9.2)	3.4 (4.7)	1.9 (3.7)	1.4 (2.3)	0.7 (1.5)	0 (0)	3.2 (3.4)	0.5 (1.4)	0.2 (0.4)	193	6.
Arthropoda: Cirripedia larvae	1 (0)	0 (0)	0.8 (1.3)	0.5 (1.1)	1.5 (2.4)	0 (0)	0.6 (0.5)	1.3 (1.9)	0.3 (0.8)	0.3 (0.7)	88	2.
Chaetognatha: Sagittoidea	1 (1.4)	0 (0)	0.2 (0.8)	0.7 (1.3)	1.3 (2.1)	0.5 (1.2)	2.6 (2.4)	0.4 (0.9)	0 (0.2)	0.3 (0.7)	75	2.
Ciliophora	0 (0)	0 (0)	0 (0)	0 (0)	0.6 (1.6)	0 (0)	6.4 (14.3)	0 (0)	0 (0)	0 (0)	46	1.
Annelida: Polychaeta larvae/juvenile	0 (0)	0 (0)	0.1 (0.3)	0.3 (1)	0.1 (0.3)	0.2 (0.8)	0.4 (0.5)	0.3 (0.7)	0.4 (0.8)	0.3 (0.7)	31	1.
Arthropoda: Brachiuran larvae	0 (0)	1 (1.4)	0.5 (0.9)	0.1 (0.3)	0.2 (0.7)	0.2 (0.6)	0 (0)	0.3 (0.4)	0.1 (0.3)	0.1 (0.3)	25	0.
Nematoda	0 (0)	0 (0)	0 (0)	0.1 (0.5)	0 (0.2)	0.3 (0.6)	0.2 (0.4)	0.4 (0.7)	0.2 (0.5)	0 (0)	19	0.
Arthropoda: Amphipoda	1 (1.4)	0 (0)	0 (0)	0 (0)	0 (0.2)	0 (0)	0.2 (0.4)	0 (0)	0 (0.2)	0.3 (1)	8	0.
Arthropoda: Decapoda (*Emerita* sp)	0 (0)	0 (0)	0 (0)	0 (0)	0.2 (0.5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	4	0.
Unidentified	5.5 (2.1)	11.5 (6.4)	4.5 (4.6)	4.3 (4)	2.2 (3.4)	3.2 (4.8)	4.8 (3.8)	3 (2.9)	2.5 (3.1)	0.6 (0.9)	386	12.
Average number of prey items	47.5 (9.3)	47 (4.5)	35.2 (2.6)	32.8 (3.1)	34.7 (2.6)	18.3 (1.3)	24 (1.8)	18.2 (1.1)	12 (1.1)	23.1 (1.9)	29.3	

3

Table 2(on next page)

Results of A) the PERMANOVA analysis on the differences in the structure of the diet of *Stomolophus meleagris* among months and seasons and B) pair-wise tests for differences between pairs of months in each season.

Significant factors (α = 0.05) are highlighted in bold.

1 Table 2. Results of A) the PERMANOVA analysis on the differences in the structure of the diet
2 of *Stomolophus meleagris* among months and seasons and B) pair-wise tests for differences
3 between pairs of months in each season. Significant factors ($\alpha = 0.05$) are highlighted in bold.

A	Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
	Season	1	10841	10841	2.2673	0.134	917
	Month(season)	5	24981	4996	2.4719	**0.001**	998
	Res	105	212230	2021			
	Total	111	249810				
B	Months	Season			T	P(perm)	perms
	February, March	1			1.440	0.077	999
	February, April	1			1.427	0.087	999
	February, May	1			1.395	0.083	998
	March, April	1			1.717	**0.017**	999
	March, May	1			1.510	**0.041**	999
	April, May	1			0.982	0.486	997
	February, March	2			2.101	**0.004**	999
	February, April	2			1.830	**0.016**	998
	March, April	2			1.270	0.151	999

4

5

Table 3(on next page)

Results of the model fitting procedure on the relationship of the body size of *Stomolophus meleagris* and its symbionts

Pr.Var.: proportion of variability explained by the model.

1 Table 3. Results of the model fitting procedure on the relationship of the body size of
2 *Stomolophus meleagris* and its symbionts. Pr.Var.: proportion of variability explained by the
3 model.

Associates	Model	a (SE)	b (SE)	Pr. Var.	F-value	p
Fish	$Y=aX^b$	1.551 (1.202)	0.809 (0.189)	0.291	134.763	<0.001
All	$Y=aX^b$	1.775 (1.371)	0.775 (0.189)	0.269	138.378	<0.001
H. zelotes	$Y=aX^b$	1.204 (0.486)	0.830 (0.098)	0.634	412.441	<0.001

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5

Table 4(on next page)

List of published (a) and new (b) reports on symbionts of the cannonball jellyfish *Stomolophus meleagris*.

An unidentified cestode larva was reported by Phillips & Levin (1973), though it is not included in the list.

1   Table 4. List of published (a) and new (b) reports on symbionts of the cannonball jellyfish *Stomolophus meleagris*. An unidentified

2   cestode larva was reported by Phillips & Levin (1973), though it is not included in the list.

Class: family	Species	Locality and literature source
(a)		
Actinopterygii: Carangidae	*Chloroscombrus chrysurus* (Linnaeus, 1766)	Mississippi Sound, Mississippi, USA (Phillips et al. 1969)
		Wrightsville Beach, North Carolina, USA (Rountree, 1983)
		Onslow Bay, North Carolina, USA (Shanks & Graham, 1988)
		Texas USA (Baughman, 1950)
	Hemicaranx amblyrhynchus (Cuvier, 1833)	Western Golf of Mexico, USA & Mexico (Hildebrand, 1954)
	Hemicaranx zelotes Gilbert, 1898	Kino Bay, Sonora, Mexico (López & Rodríguez, 2008)
		Málaga Bay, Pacific coast, Colombia (This study)
	Caranx crysos (Mitchill, 1815)	Barataria Bay, Louisiana, USA (Gunter, 1935)
	Caranx hippos (Linnaeus, 1766)	Wrightsville Beach, North Carolina, USA (Rountree, 1983)
	Carangoides bartholomaei (Cuvier, 1833)	Wrightsville Beach, North Carolina, USA (Rountree, 1983)
Actinopterygii: Stromateidae	*Peprilus triacanthus* (Peck, 1804)	Wrightsville Beach, North Carolina, USA (Rountree, 1983)
		Beaufort, North Carolina, USA (Smith, 1907)
		Port Aransas, Texas, USA (Hoese et al. 1964)
		Western Golf of Mexico, USA & Mexico (Hildebrand, 1954)
		Gulf of Mexico, USA (Horn, 1970)
	Peprilus burti Fowler, 1944	Gulf of Mexico, USA (Horn, 1970)
	Peprilus paru (Linnaeus, 1758)	Mississippi Sound, Mississippi, USA (Phillips et al. 1969)
		Port Aransas, Texas, USA (Hoese et al. 1964)
Actinopterygii: Monacanthidae	*Stephanolepis hispida* (Linnaeus, 1766)	Mississippi Sound, Mississippi, USA (Phillips et al. 1969)
		Wrightsville Beach, North Carolina, USA (Rountree, 1983)
		Onslow Bay, North Carolina, USA (Shanks & Graham, 1988)
	Aluterus schoepfii (Walbaum, 1792)	Wrightsville Beach, North Carolina, USA (Rountree, 1983)
		Woods Hole, Massachusetts, USA (Hargitt, 1905)
Actinopterygii: Nomeidae	*Nomeus gronovii* (Gmelin, 1789)	Beaufort, North Carolina, USA (Smith, 1907)
		Japan & Hong Kong (Morton, 1989)

Malacostraca: Epialtidae	*Libinia dubia* H. Milne Edwards, 1834	Beaufort, North Carolina, USA (Gutsell, 1928)
		Mississippi Sound, Mississippi, USA (Phillips et al. 1969)
		South Carolina, USA (Corrington, 1927)
		Wrightsville Beach, North Carolina, USA (Rountree, 1983)
		Onslow Bay, North Carolina, USA (Shanks & Graham, 1988)
		Fort Pierce, Florida, USA (Tunberg & Reed, 2004)
	Libinia sp	Texas coast, USA (Whitten, Rosene & Hedgpeth, 1950)
	*Libinia emarginata,*Leach, 1815	Western Golf of Mexico, USA & Mexico (Hildebrand, 1954)
Malacostraca: Portunidae	*Charybdis (Charybdis) feriata* (Linnaeus, 1758)	Japan & Hong Kong (Morton, 1989)
Hexanauplia: Lepadidae	*Conchoderma virgatum* Spengler, 1789	Guaymas, Mexico (Álvarez-Tello et al. 2013)
Cestoda: Otobothriidae	*Otobothrium dinoi* (Mendez, 1944) Palm, 2004	Cananéia, Sao Paulo, Brazil (Vanucci 1954)
(b)		
Actinopterygii: Carangidae	*Chloroscombrus orqueta* Jordan & Gilbert, 1883	Málaga Bay, Pacific coast, Colombia
	Oligoplites altus (Günther, 1868)	Málaga Bay, Pacific coast, Colombia
	Selene brevoortii (Gill, 1863)	Málaga Bay, Pacific coast, Colombia
Actinopterygii: Atherinopsidae	*Atherinella argentea* Chernoff, 1986	Málaga Bay, Pacific coast, Colombia
Actinopterygii: Gerreidae	*Gerres simillimus* Regan 1907	Málaga Bay, Pacific coast, Colombia
Actinopterygii: Centropomidae	*Centropomus medius* Günther, 1864	Málaga Bay, Pacific coast, Colombia
Actinopterygii: Hemiramphidae	*Hyporhamphus snyderi,* Meek & Hildebrand, 1923	Málaga Bay, Pacific coast, Colombia
Actinopterygii: Lutjanidae	*Lutjanus guttatus* (Steindachner, 1869)	Málaga Bay, Pacific coast, Colombia
Malacostraca: Penaeidae	*Penaeus stylirostris* Stimpson, 1871	Málaga Bay, Pacific coast, Colombia
Cephalopoda: Loliginidae	*Lolliguncula (Lolliguncula) panamensis* Berry, 1911	Málaga Bay, Pacific coast, Colombia

3